Phylogeny and Evolution of the Larval Diet in the Sciaroidea (Diptera, Bibionomorpha) since the Mesozoic

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ABSTRACT

The larvae of the Keroplatidae exhibit diverse trophic specializations, being either ferocious predators, killing their prey by way of toxic diffuse nets, or fungivorous insects, spinning sheet-like webs to gather the spores of polyporous fungi. Previous studies of trophic specializations of larvae in Sciaroidea have been based up to now on inference from morphology or on empirical demonstration. These have led to the general notion that fungivory is ancestral for the Sciaroidea and predation ancestral for the Keroplatidae. New phylogenies for Sciaroidea and Keroplatidae are proposed here; the Cecidomyiidae seem to be the sister-group of all other families. Seven attributes are mapped on the cladograms – endobiosis/epibiosis, fungivory/other diets, presence or absence of silk secretion, predation/sporophagy, labial secretion pH ± 3, net-like/sheet-like web, optobiosis/cryptobiosis. It is concluded that fungivory and silk secretion are ancestral for Sciaroidea and predation ancestral for the Keroplatidae while sporophagy is a specialization derived from predation. Epibiosis, with its cryptobiotic specialization, the net-like web and the highly acid pH, are also apomorphic for Keroplatidae. Sporophagy, optobiosis, sheet-like web and less acid pH are correlated apomorphic traits for the tribe Keroplatini. The fossil and biogeographical data allow dating most of these specializations back to at least the Lower Cretaceous.

RÉSUMÉ

Phylogénie et évolution du régime alimentaire des larves de Sciaroidea (Diptera, Bibionomorpha)

Les larves de Keroplatidae présentent un régime alimentaire très contrasté, puisque les unes sont de redoutables prédateurs qui tuent leurs proies au moyen d'une salive toxique répandue dans une toile de chasse, tandis que les autres sont inféodées aux Polypores, dont ils recueillent les spores dans une toile de récolte. La question des spécialisations trophiques chez les larves de Sciaroidea a jusqu'ici été abordée par des voies empiriques ou morpho-anatomiques, qui on conduit à penser notamment que la mycophagie était ancestrale pour les Sciaroidea et la prédation ancestrale pour les Keroplatidae. De nouvelles phylogénies des Sciaroidea, puis des Keroplatidae, sont proposées dans ce travail ; les Cecidomyiidae apparaissent comme le groupe-frère de l'ensemble des autres familles de Sciaroidea. Sept attributs sont superposés aux cladogrammes – endobiose/épibiose, mycétophagie *s.l.*/autres régimes, sécrétion de soie ou non, prédation/sporophagie, sécrétion labiale à pH±3, toile en réseau/nappe, optobiose/cryptobiose. On est amené à conclure que la mycétophagie et la sécrétion de soie sont ancestrales pour les Sciaroidea et la prédation ancestrale pour les Keroplatidae, tandis que la sporophagie de ces derniers est une spécialisation développée à partir de la prédation. L'épibiose avec sa spécialisation en cryptobiose, la toile en réseau et le pH hautement acide, sont également plésiomorphes pour les Keroplatidae. Sporophagie, optobiose, toile en nappe et pH moins acide sont des apomorphies corrélées de la tribu des Keroplatini. La datation de l'ensemble des cladogrammes par les fossiles

et les données biogéographiques permet en outre d'attribuer à la plupart de ces spécialisations un âge au moins Crétacé inférieur.

INTRODUCTION

The larvae of the Keroplatidae, a family of Sciaroidea, have highly diverse food preferences. Some are formidable predators, killing their prey by means of a toxic highly acidic saliva dispersed on a trapping net-like web, while others are live under bracket-fungi (Polyporaceae), where they gather spores in a sheet-like, less acidic web. Some lead a cryptic life, deeply hidden at maximum darkness and humidity (a way of life for which the term *cryptobiosis* is proposed), while others, while they do not shun obscurity, are able to live more or less in the open (*optobiosis*) if necessary.

Trophic specialization of the larvae of Sciaroidea has up to now been addressed empirically (KRIVOSHEINA, 1969; LASTOVKA, 1972; JACKSON, 1974), or through morpho-anatomy (ZAITSEV, 1983, 1984a, b; MATILE, 1986). These works led to the conclusion that fungivory was ancestral for Sciaroidea, and predation ancestral for the Keroplatidae. LASTOVKA (1972), who noted that fungivory is most common, and therefore plesiomorphic, also assumed that predation probably evolved from sporophagy.

I propose in this paper to test these previous hypotheses in the light of phylogeny, to study attributes (in the sense of BROOKS & MCLENNAN, 1991) linked to food preference in the Sciaroidea, especially the Keroplatidae. The following questions will be addressed: What was the ancestral food of the Keroplatidae larvae? What was the ancestral condition of their web? Was their common ancestor a cryptobiont or an optobiont? Moreover, it has been demonstrated by historical biogeography and by fossil data, that Keroplatidae already existed at least in the Upper Jurassic (MATILE, 1990; GRIMALDI, 1990; EVENHUIS, 1994). I shall try to date the appearance of these attributes by means of fossil and palaeogeographic data.

According to some authors who have recently addressed the problem of the classification of the Sciaroidea (or Mycetophiloidea), the superfamily consists of three families only – Mycetophilidae, Sciaridae and Cecidomyiidae (WOOD & BORKENT, 1989; COLLESS & MCALPINE, 1991) – the last two being sister-group to the first (WOOD & BORKENT, 1989). In a recent paper (OOSTERBROEK & COURTNEY, 1995), the superfamily is suppressed as such and included in the Bibionoidea, while the Mycetophilidae, Sciaridae and Cecidomyiidae show the same relationships proposed in WOOD & BORKENT's paper. Nevertheless, in all three of these papers (Fig. 1), the paraphyly of the adopted concept of "Mycetophilidae" is explicitly recognized.

On the other hand, authors who have treated fossil as well as recent taxa recognize more readily a group of "Mycetophilidae" families, sister-group to the Sciaridae, and then sister-group to the Cecidomyiidae, this last family treated by some as the superfamily Cecidomyioidea (ROHDENDORF, 1964, 1974; KOVALEV, 1987a; SHCHERBAKOV *et al.*, 1995). Many authors have treated the subfamilies of EDWARDS (1925) – Ditomyiinae, Diadocidiinae, Keroplatinae, Bolitophilinae, Mycetophilinae, Lygistorrhininae and Sciarinae – as of family rank like the Cecidomyiidae, but phylogenetically oriented papers are scarce (HENNIG, 1954, 1968, 1973; MATILE, 1986, 1990; AMORIM, 1992; Fig. 1). I have pointed out elsewhere (MATILE, 1993) that it might not be phylogenetically sound to use only three families "in keeping with North American tradition" (WOOD & BORKENT, 1989); neither do I feel dogmatic in thinking "that a
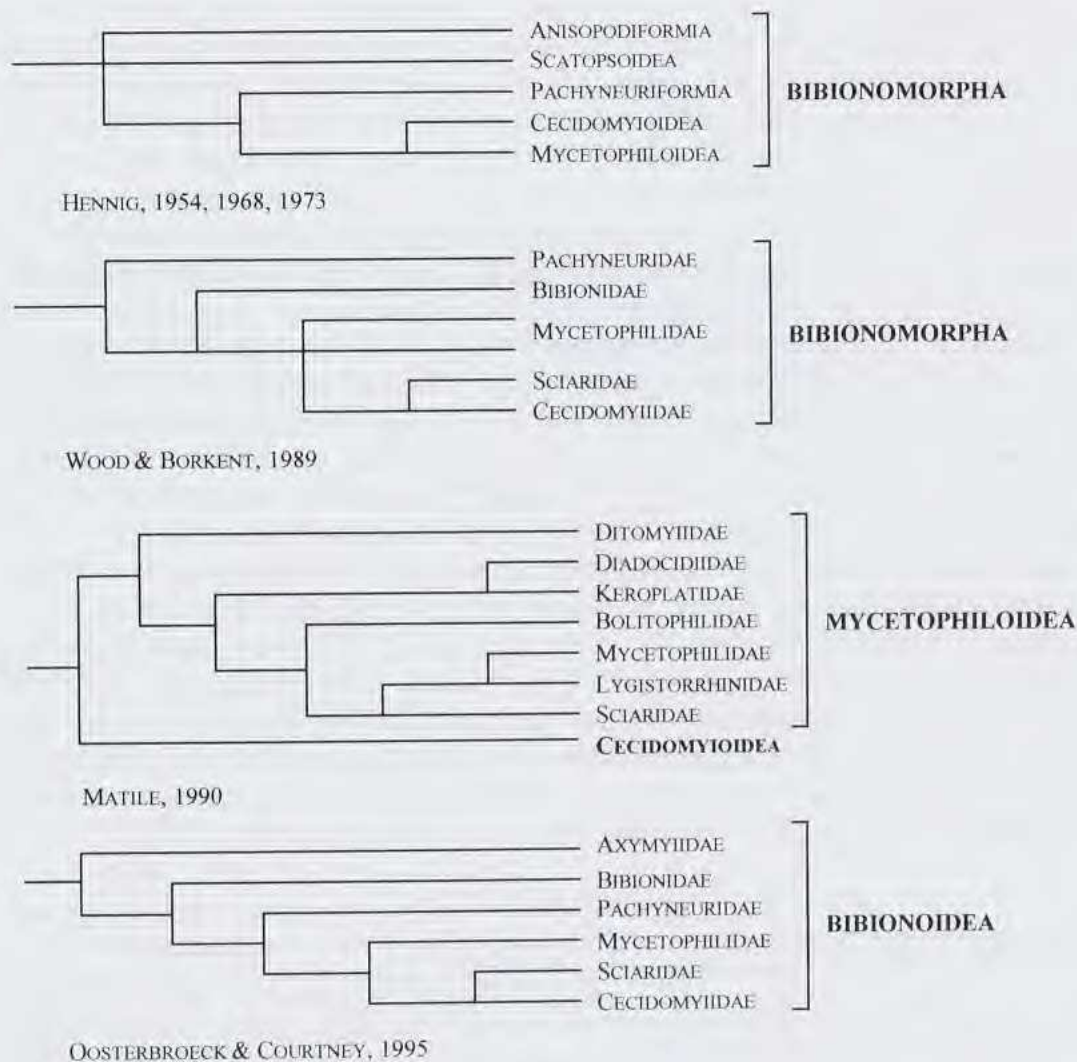
Fig. 1. — Hypotheses on the phylogeny of the Bibionomorpha, or the Mycetophiloidea + Cecidomyioidea, according to HENNIG (synthesis of 1954, 1968, 1973); WOOD & BORKENT, 1989; MATILE, 1990; OOSTERBROECK & COURTNEY, 1995.

paraphyletic taxon cannot be a perfectly good one" (COLLESS & MCALPINE, 1991), especially for the kind of analyses presented here or in historical biogeography.

A hypothesis of relationships of the families of Sciaroidea (Cecidomyiidae excluded) has been given by MATILE (1986,1990) (for a review of earlier hypotheses see MATILE, 1986: 376-410), where the Sciaridae are considered the sister-group of the Mycetophilidae + Lygistorrhinidae (Fig. 1). In this paper, a new hypothesis founded on a greater number of characters is proposed for the Sciaroidea.

Most larvae of Sciaroidea are more or less narrowly linked to the carpophores of the higher fungi, either spinning a web under or close to the hymenium (all Diadocidiidae, certain Keroplatidae and Mycetophilidae), or living in the carpophore itself (some Ditomyiidae, all Bolitophilidae, most Mycetophilidae, some Sciaridae). They feed on spores only (sporophagy, fungivory *sensu lato*), on spores and hyphae, and perhaps in some cases on hyphae only. Some species live in rotten wood, where they feed on mycelia (some Ditomyiidae and Sciaridae). On the other hand, most Sciaridae live in the soil litter, were they are thought to be saprophagous. Some very few species of Sciaridae and Mycetophilidae are phytophagous, while many Keroplatidae and some Mycetophilidae are predaceous. Most Cecidomyiidae larvae are phytophagous, but there are predatory or fungivorous species.

A number of traits are more or less narrowly associated with larval feeding habits: secretion of silky threads to spin webs and/or pupal cocoons, endobiosis or epibiosis and, in epibiosis structure and composition of the web. PLACHTER (1979b) assumed that the three-dimensional web of certain Keroplatidae species was derived from a primitive, less complex web with a wide central band. ZAITSEV (1984) thought that the first step towards fungivory in Sciaroidea had been epibiont "grazers" feeding on mycelia covering wood, leaves, and other substrata. In a previous work, the larval morpho-ecology of the Sciaroidea was studied. The ancestral stock of the superfamily was presumed to be a eurybiont detritophilous larva in the sense of MAMAEV (1968, 1975), *e.g.* a fungivorous larva of soil, litter and rotting wood, without silk secretion and bearing well-developed antennae and body macrochaetae (MATILE, 1986). The groundplan of the Diadocidiidae-Keroplatidae clade and its sister-group has been inferred as having an endobiont larva, to be fungivorous and silk-producing, and to have a smooth and long body, with vestigial antennae, eyes and macrochaetae, however these provisional conclusions were not published in my 1990 monograph.

MATERIALS AND METHODS

The imaginal morphological data used in the phylogenetic hypotheses discussed here was provided mainly by material from the Collections of the Muséum National d'Histoire naturelle, Paris. The remainder came from specimens loaned by many colleagues and institutions worldwide (*cf.* MATILE, 1990: 24-25, 637). I have thus been able to examine adults of representative species (most often at least the type-species) of practically every known genus of Sciaroidea, with the notable exception of the Sciaridae, where only the largest genera have been checked. Data on the Cecidomyiidae were mostly obtained from the literature.

Concerning the name of Sciaroidea versus Mycetophiloidea, the superfamily name Sciaroidea is founded on *Sciaraedes* Billberg, 1820, while Mycetophiloidea is based on *Mycetophilites* Newman, 1834 (SABROSKY, pers. com.). Although names of the family-group using the prefix Mycetophil- are many times more numerous than those founded on Sciar-, art. 36a (Principle of coordination for the family-group names) of the International Code of Zoological Nomenclature imposes the use of Sciaroidea, unfortunately resurrected from a long oblivion by McALPINE *et al.* (1981).

As regards larvae, this paper is based on published works, especially those by MADWAR (1937), BRAUNS (1954a) and PLACHTER (1979a, 1979b, 1979c) for illustrations and observations, and by LASTOVKA (1972), ZAITSEV (1984) and MATILE (1986, 1990) for interpretation and homology. Personal observations, published or not, have been added – these have been accumulated over thirty years, in the field and in the laboratory, in tropical and temperate areas.

Concerning the polarization of characters, the analysis by MATILE (1990) has generally been followed; it bears mainly on Keroplatidae, but can easily be extended to the Sciaroidea. The matrices of characters have been treated by the Hennig86 program (FARRIS, 1988), with implicit enumeration ("ie" command), characters non-ordered ("cc-" command), and the evolution of the characters has been followed with the Clados program (NIXON, 1991). After phylogenetic hypotheses for the groups involved were obtained, it was possible to proceed to an optimization (FARRIS, 1970) of the different attributes on the cladograms. The seven attributes studied are identified and numbered in the text; the first three bear on the Bibionomorpha and Sciaroidea, the last four on Keroplatidae only.

PHYLOGENY

The few phylogenetic hypotheses expressed up to now on Sciaroidea have been manually obtained, except in OOSTERBROECK & COURTNEY'S analysis, which bears on all families of "Nematocera", and was done using the programs Paup and Hennig86. All hypotheses – autapomorphic family traits excluded – have taken few characters into consideration: 4 IN WOOD & BORKENT's, 8 in OOSTERBROECK & COURTNEY's, 9 in MATILE's. I have been able to gather a greater number of characters (30), either new or already available in the literature, which allows the reconstruction of a new cladogram (although yet provisional) of the Sciaroidea.

Appendix I refers to these characters and their matrix, and gives the references to their polarization when already published. The outgroups chosen are the Bibionidae (genus *Bibio* Geoffroy) and the Pachyneuridae (genus *Cramptonomyia* Alexander), both basal to the Bibionomorpha in WOOD & BORKENT's and OOSTERBROEK & COURTNEY's cladograms. *Cramptonomyia* (here Pachyneuridae) and *Hesperinus* Walker (Bibionidae), *Plecia* Meigen and allied genera (Bibionidae) are sometimes considered as of family rank. The position of the Pachyneuridae is debatable. For example the family has been placed with Axymiidae and others in an infraorder Axymyiomorpha (WOOD & BORKENT, 1989) or a superfamily Pachyneuroidea (KRZEMINSKA *et al.*, 1993). For other authors Axymiidae stand by themselves in Axymyioidea (SHCHERBAKOV *et al.*, 1995), or the group Cramptonomyiformia is proposed (AMORIM, 1992), etc. (see review in AMORIM, 1992). The reader is therefore reminded that I do not purport to give here a new hypothesis on the phylogeny of the Bibionomorpha – the introduction in the cladogram of a genus each of Bibionidae and Pachyneuridae derives from the necessity of choosing at least two outgroups. The Cecidomyiidae have been taken into account because of their presumed sister-group relationship with the Sciaridae rather than the rest of the Sciaroidea.

Autapomorphies of the families have been excluded from the analysis, as well as those of the Bibionomorpha. We have not used OOSTERBROECK & COURTNEY's character 90 (absence of sperm pump), because it is present at least in some Keroplatidae (MATILE, 1990). Their character 72 (anterior veins concentrated along costal margin) has also been eliminated because this costalization is common in Keroplatidae and Mycetophilidae.

Phylogenetic analysis in Hennig86 gave only one most parsimonious tree, length 44, CI = 0.70 and RI = 0.76 (Fig. 2). This tree shows the Cecidomyiidae as the sister-group of the Ditomyiidae+ group (terminology of AMORIM, 1982) as advocated, although with some doubts, by HENNIG (1954, 1970, 1973). The structure of the Ditomyiidae+ group agrees with the cladogram of the "Mycetophiloidea" given by MATILE (1990), and there seems no necessity to retain the Cecidomyiidae as a superfamily by themselves. The cladogram agrees also with the phylochronogram given by SHCHERBAKOV *et al.* (1995) as regards the recent families, and especially the sister-group relationship of Cecidomyiidae and Sciaroidea.

It is to be noted that several characters are yet unknown in some terminal taxa, especially number 14 (loss of dorsal transverse connective in larval tracheal system), 29 (chromosomic elimination) and 30 (loss of central sperm microtubule). The cladogram implies that character 14 has appeared by homoplasy in Sciaridae and Cecidomyiidae, and that characters 29 and 30 are basal for the Bibionomorpha, with a reversal in the clade Mycetophilidae-[Lygistorrhinidae].

The Keroplatidae have been divided into three subfamilies, Arachnocampinae, Macrocerinae and Keroplatinae (MATILE, 1981a). In addition, two tribes have been recognized in
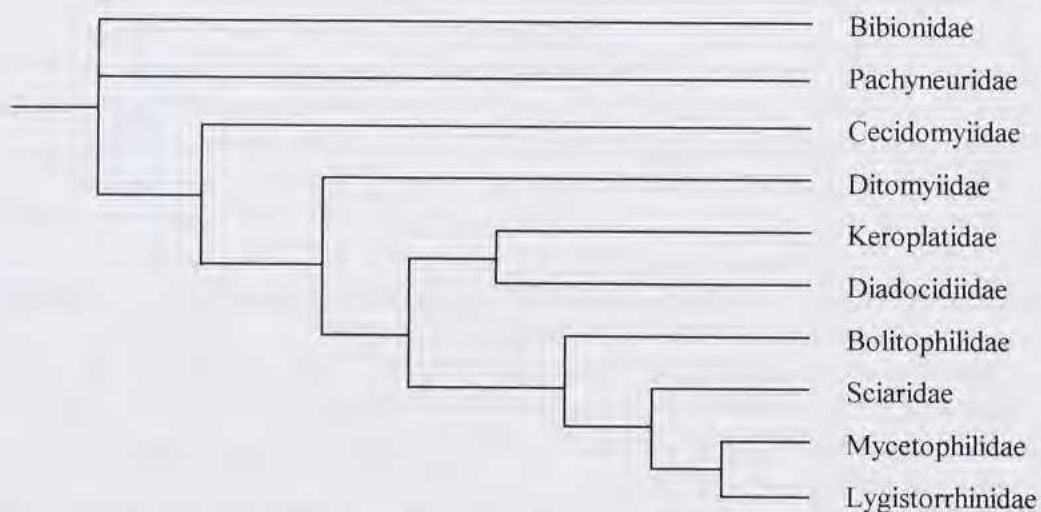
FIG. 2. — Phylogenetic relationships of the Sciaroidea. Hennig86, 30 characters, unordered, "ie" command. Length: 44, CI = 0.70, RI = 0.76.

the last two subfamilies: Macrocerini and Robsonomyini in Macrocerinae, and in Keroplatinae Keroplatini and Orfeliini (MATILE, 1990). A phylogenetic analysis of these three families has been given in MATILE ,1990, on the basis of 40 larval, pupal and imaginal characters. This analysis was hand-treated, and I present here a quantitative analysis bearing on 45 characters (without the two tribes of Macrocerinae, the larvae of only *Macrocera* being known). The outgroup chosen is the family Ditomyiidae. The characters, polarized after MATILE, 1990, and their matrix are given in Appendix II. The treatment of the matrix by Hennig86 gave only one tree, length 45, with high indices – CI = 0.97, RI = 0.93 (Fig. 3). The tree has the same structure than that published in 1990.

Arachnocampinae are monogeneric and only the larvae of *Macrocera* Meigen are known in Macrocerinae. We possess larval data for only 15 out of the 73 present genera of Keroplatinae (in fact 17, but for two genera, *Platyroptilon* Westwood and *Neoceroplatus* Edwards, the data are incomplete). This lack of knowledge is not surprising since one of the attributes of many Keroplatidae is precisely cryptobiosis... To leave out unnecessary noise (and pending a generic revision of the Orfeliini, an enterprise which should take several years), the analysis has been pursued only on the following 15 genera: 5 genera of Keroplatini (*Cerotelion* Fabricius, *Heteropterna* Skuse, *Keroplatus* Bosc, *Mallochinus* Edwards, *Tergostylus* Matile) and 10 genera of Orfeliini [*Neoditomyia* Lane & Stürm, "*Neoplatyura*" *fultoni* (Shaw), which should probably be given a genus by itself, *Orfelia* Costa, *Planarivora* Hickman, *Platyceridion* Tollet, *Platyura* Meigen, *Proceroplatus* Edwards, *Truplaya* Edwards, *Urytalpa* Edwards, *Xenoplatyura* Malloch].

Appendix III lists the 14 characters (generic autapomorphies excluded) used in the analysis of the Keroplatini with known larvae and their matrix. *Arachnocampa* is used as the outgroup.

The matrix treated by Hennig86 gave only one tree, length 19, CI = 84, RI = 86. The tree (Fig. 4) is not different from the one which can be deduced from the general cladogram of the Keroplatini proposed in MATILE (1990).
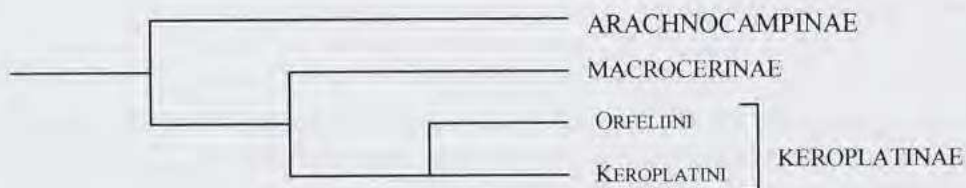
FIG. 3. — Phylogenetic relationships among subfamilies and tribes of Keroplatidae. Hennig 86, "ie" command, 45 characters. Length: 45, CI = 0.97, RI = 0.93.
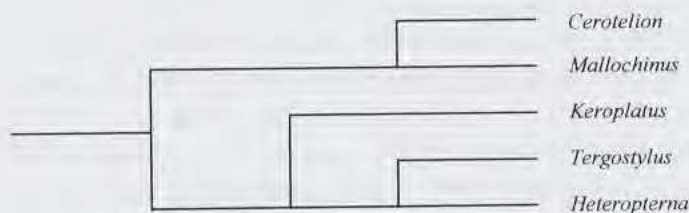
FIG. 4. — Phylogenetic relationships among five genera of Keroplatini. Hennig 86, 14 characters, "ie" command, unordered. Length: 19, CI = 0.84, RI = 0.86.
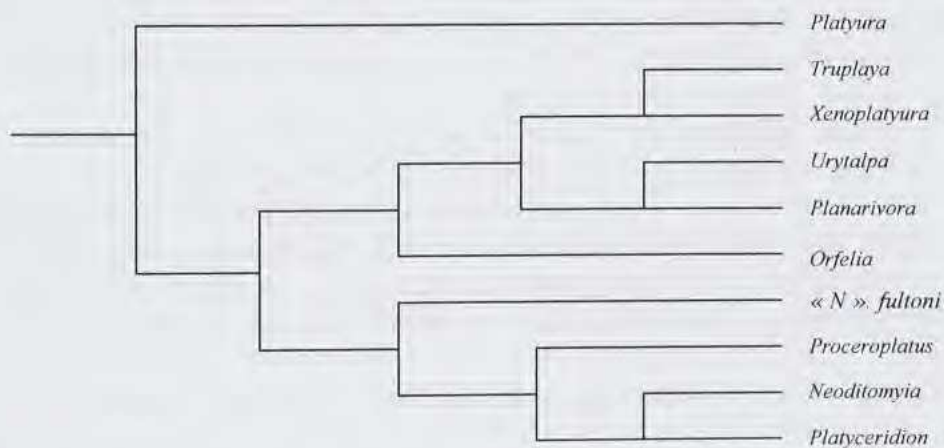
FIG. 5. — Phylogenetic relationships among ten genera of Orfeliini. Hennig86, 23 characters, "ie" command, unordered. Length 42, CI = 0.57, RI = 0.66.

Twenty-seven characters (generic autapomorphies excluded) have been used in the phylogenetic analysis of the 10 Orfeliini genera with known larvae; they are listed in Appendix IV, with the corresponding matrix. *Arachnocampa* has been chosen as the outgroup. Hennig86 gave only one tree, length 42, CI = 0.57, RI = 0.66 (Fig. 5).

The studied Orfeliini fall readily in two sister-clades, *Orfelia*+ and "*N.*" *fultoni*+, with *Platyura* being their sister-group.

ATTRIBUTES

Four attributes of the larvae of Keroplatidae will be studied. In order to study the evolution of the food-linked traits of this family, it is first necessary to consider them at the superfamily level, as well as in the outgroups chosen.

A study of the Bibionomorpha as a whole leads to the consideration of three attributes, which will be useful in the following analyses:

Endobiosis vs epibiosis. Endobiont larvae live inside their source of food, epibiont larvae live outside their source of food.

Fungivory sensu lato *vs various other preferences.* Fungivorous larvae feed on hyphae and/or spores inside the fruiting bodies of higher fungi, or on mycelium in rotten wood or litter, or feed exclusively on spores falling from the hymenium of Polyporaceae. These three categories belong to fungivory *s.l.*

Silk secretion. Many larvae secrete silk for various purposes, and at least for the building of the last instar cocoon, in which the larva will pupate. Others have no silk secretion and naked pupae.

The attributes of the Keroplatidae to be studied are as following:

Predation vs sporophagy. These terms are self-explanatory, taking into account that the "fungivory" of Keroplatidae is restricted to spores escaping from the hymenium of bracket-fungi.

Net-like web vs sheet-like web. Some keroplatid larvae spin a diffuse, three-dimensional web bearing fishing lines (Figs 6, 8, 10). Others secrete a wide, mostly two-dimensional web (Fig. 7).

pH of web. The webs spun by the larvae bear drops of an acid labial fluid; according to species, the pH stands between 1 and 2.7 or, in other cases, is higher than 3.

Cryptobiosis vs optobiosis. These new terms are coined for epibiont larvae living in hidden, obscure and water saturated cavities, such as under stones or rotting trunks, in phytotelma, etc. (cryptobionts). In contrast, other epibiont larvae live more in the open, on the walls of caves, under bracket-fungi, under overhanging cliffs or stream banks, under leaves, etc. (optobionts).

Bibionid larvae are mostly scavengers or plant-feeding, living in the soil on roots, grasses and decaying plant material (HARDY, 1981, and references therein). Larvae of Pachyneuridae are associated with rotten wood (VOCKEROTH, 1974; KRIVOSHEINA & MAMAEV, 1988); whether they are true xylophagous insects or feed on mycelia inside the wood has not been ascertained.

Most Cecidomyiidae larvae are plant-feeding and gall-forming, but the more basal are fungivorous (MAMAEV, 1975; GAGNÉ, 1986). There are also some endoparasites and some predatory species on insects and mites, a habit that evolved separately several times according to GAGNÉ (this author has also noted the anatomo-morphological exaptations to plant-feeding shown by the "ancestral" fungus-feeding species – sucking mouthparts, extra-intestinal digestion and spatula). Cecidomyiidae larvae are epibionts or endobionts and most secrete silk at least for the cocoon in which they will pupate.

In the Ditomyiidae, larvae of *Ditomyia* Winnertz feed on hard bracket-fungi such as *Coriolus versicolor* and others, and those of *Asioditomyia japonica* (Sasakawa) have been found in *Lenzites betulina*. *Symmerus* Walker and *Australosymmerus* Freeman are said to be xylophagous (MADWAR, 1937; MUNROE, 1974); however CHANDLER (1993) cites *Symmerus annulatus* (Meigen) reared from a hard ascomycete fungus, *Hypoxylon rubiginosum*. The term "frass" referred to by MUNROE for the substance left in their galleries by larvae of *S. coqulus* Garrett is ambiguous, since it can apply to either larval excrement or saw dust left by xylophagous animals. It is very possible that all Ditomyiidae larvae found in rotten wood feed on the mycelia that it contains. There is no pupal cocoon, the pupation takes place in the substratum.

Feeding habits of the larvae of Diadocidiidae have been uncertain for a long time (BRAUNS, 1954a). I have often observed them under rotten wood invaded either by mycelia or by encrusting Polyporaceae. In specimens killed in fixative fluid, spores desegregating progressively towards the rear of body were observed, and the discovery of *Diadocidia ferruginosa* (Meigen) on *Peniophora* sp. (CHANDLER, 1993) confirms the fungivory of the family. Diadocidiid larvae are epibionts and spin a silky tube and a pupal cocoon.

Bolitophilidae have strictly endobiont fungicolous larvae and breed mostly in Strophariaceae, Cortinariaceae, Polyporaceae and Boletaceae (HUTSON *et al.*, 1980). They spin neither web nor pupal cocoon.

Keroplatidae comprise either predators or sporophagous larvae, rarely species showing a mixed diet (*cf.* MATILE, 1986, 1990). *Cerotelion*, a normally sporophagous species, has been recorded once as feeding on a recently dead larva, and once as cannibalistic (a pupa of its own species) (MANSBRIDGE, 1933). However, these observations on *Cerotelion* have been made in breeding jars where spores can get scarce, or disappear. On the other hand, first instar larvae of *Macrocera nobilis* Johnson are scavengers, and the following instars are predators (PECK & RUSSEL, 1976). All larvae of Keroplatidae spin webs and are epibionts, except those of the genus *Planarivora* Hickman, or at least of their Tasmanian representative, *Planarivora insignis* Hickman, which is an endoparasitoid of land planarians, but nonetheless spins a pupal cocoon after emerging from its dead host (HICKMAN, 1965).

The food preferences of mycetophilid larvae are very diverse, ranging from predation, with epibiont web-spinning species, to phytophagy (but exclusively linked with liverworts – in two clades: Mycomyinae and Gnoristinae.), through true fungivory, the most common diet. Most known larvae live in a hygroscopic web, except in subfamily Mycetophilinae. Almost without exception there is a pupal cocoon (*Speolepta* Edwards, no cocoon; some Mycetophilini genera, a pupal case).

Sciaridae comprise some true fungivorous, phytophagous, coprophagous and xylophagous species, but mostly they are litter forms, where they probably feed on mycelia (STEFFAN, 1981). They spin webs and pupal cocoons.

The feeding habits of the studied families of Bibionomorpha are summarized in Table I. The term "xylophagous" has been put between brackets because it is not known with certainty if larvae of Pachyneuridae, some Ditomyiidae and some Sciaridae are really wood-eating, or rather feed on mycelia in rotten wood.

TABLE 1. — Food preferences of the larvae of Bibionomorpha. Legends: end/epi = endo- or epibionts; silk = silk secretion; [xylo] = xylophagous; pred. = predators; fungic. = fungicolous; creo-fung. = creo-fungicolous; phytoph. = phytophagous; saproph. = saprophagous; parasit. = parasitoids. liverw. = liverworts.

Families	Food								
	end/epi	silk	[xylo.]	pred.	fungic.	creo-f.	phytoph	saproph	parasit.
Bibionidae	end	0	0	0	0	0	+	+	0
Pachyneuridae	end	0	+	0	?	0	0	0	0
Ditomyiidae	end	0	+	0	+	0	0	0	0
Diadocidiidae	epi	+	0	0	+	0	0	0	0
Keroplatidae	epi	+	0	+	+	+	0	0	+
Bolitophilidae	end	0	0	0	+	0	0	0	0
Mycetophilidae	end/epi	+	0	+	+	0	liverw.	0	0
Sciaridae	end/epi	+	+	0	+	0	0	+	0
Cecidomyiidae	end/epi	+	0	+	+	+	+	0	+

Larvae of Keroplatidae have very diverse feeding habits. Members of the Arachnocampinae (monogeneric), and *Macrocera* in Macrocerinae (first instars of all other genera are unknown) are predators of insects and other small invertebrates, first instar larvae of at least one species of *Macrocera* being scavengers. In the Keroplatinae, known Orfeliini are predators (*Neoditomyia, "Neoplatyura" fultoni, Orfelia, Platyceridion, Platyura, Proceroplatus, Truplaya, Xenoplatyura*), except *Planarivora*, a parasitoid, and *Urytalpa*, feeding habit unknown (but see below). Three genera have been discovered recently, that even attack ants: *Truplaya* (KOVAC & MATILE, in press), *Proceroplatus* (AIELLO & JOLIVET, in press; MATILE, in press) and *Platyceridion* (CHANDLER & MATILE, in prep.). All known Keroplatini are spore-feeders (*Cerotelion, Heteropterna, Keroplatus, Mallochinus, Tergostylus*), with *Cerotelion*, as already noted, occasionally able to eat dead or immobile prey, at least in captivity. Two other species of Keroplatini, belonging to genera *Platyroptilon* and *Neoceroplatus*, have been found in connection with rotten wood invaded by mycelia or with bracket-fungi (DURET, 1974; MATILE, 1982), and are very probably spore-feeders.

Larvae of *Arachnocampa* and *Neoditomyia* are found in natural and artificial caves and tunnels, but also in more open conditions such as under leaves (PUGSLEY, 1984; MATILE, 1990, 1994; STÜRM, 1973; JACKSON, 1974), while Keroplatinae Keroplatini live mostly under bracket-fungi, either on standing trees or fallen trunks and branches (MATILE, 1990, and references therein). All of these are therefore optobionts. *Macrocera* larvae are cryptobionts, except in cavernicolous conditions (MATILE, 1990, 1994, and references therein). All known Orfeliini except *Neoditomyia* (tropical caves and forests) are also cryptobionts, living in deeply burrowed cavities under stones or fallen trunks, in bamboo internodes or domatia of ant-plants (PLACHTER, 1979a, 1979b; MATILE, 1990, and references therein; JOLIVET, 1996, KOVAC & MATILE, in press; AIELLO & JOLIVET, in press; MATILE, in press; CHANDLER & MATILE, in prep.).

The webs of keroplatid larvae have three more or less distinct parts: a central tube in which the larva moves when active – a shelter web, usually hidden in some secondary cavity of the substratum – and a feeding web. For predators, the feeding web comprises a more or less dense

TABLE 2. — Food preference and other attributes of larvae of Keroplatidae (pH data from PLACHTER, 1979a).

Genera	food	pH of web	net shape	cryptobiosis
Arachnocampa	predator	"very acid"	net	0
Macrocera	predator	2,4 - 2,7	net	+
Platyura	predator	1,3 - 1,6	net	+
Truplaya	predator	?	net	+
Xenoplatyura	predator	1-2	net	+
Urytalpa	?	3,6 - 4,0	net/sheet	+
Planarivora	parasitoid	?	pupa only	+
Orfelia	predator	1,3 - 1,6	net	+
"N." fultoni	predator	?	net	+
Proceroplatus	predator	?	net	+
Neoditomyia	predator	?	net	0
Platyceridion	predator	?	net	+
Cerotelion	creo-sporo.	1,3 - 1,6	net/sheet	0
Mallochinus	?	?	?	0
Keroplatus	sporoph.	3,0 - 3,4	sheet	0
Tergostylus	sporoph.	not toxic	sheet	0
Heteropterna	sporoph.	not toxic	sheet	0

system of crossed lines, from which drop "fishing lines", short or long according to the space available. Shelter and feeding webs bear numerous droplets of saliva containing oxalic acid, sometimes in very high concentration (BUSTON in MANSBRIDGE, 1933; PLACHTER, 1979a). All are individual webs, but can be re-used by later generations in some species of cave-dwelling *Macrocera* (PECK & RUSSEL, 1976). These predator systems will be called "net-webs". All have a pH of 2.7 or less. In the webs of spore eaters, the fishing net is replaced by a wide mucous film which covers the hymenium, and is often collective, sheltering larvae of several instars – these will be called sheet-webs. The saliva of at least some of these sporophagous species also contains oxalic acid. *Keroplatus* has a pH of 3 or more, but *Cerotelion* is highly acid, and has a web (Fig. 9) intermediate between the net type and the sheet type (crossed lines, but no fishing lines). Small invertebrates introduced in webs of *Tergostylus* and *Heteropterna* have shown no particular reactions (as with *Keroplatus*), and it may be inferred that their acidity is also weak. The sheet-webs of *Keroplatus tipuloides* Bosc can be re-used by later generations (MATILE, pers. obs.). All these data are summarized in Table 2.

In summary, examination of the table shows that when known, the pH is always correlated with the type of the web: 2.7 or less for net-webs (predators), 3 or more for sheet-webs (spore-feeders). *Cerotelion*, which has an intermediate web and, although spore-feeding, can show predatory behavior, at least in laboratory conditions, is an exception. It is easy to deduce from this that *Urytalpa* must be a spore-feeder. The only species whose larva is known, *U. ochracea* (Meigen), was observed "practically swimming" in its sheet-like web (PLACHTER, 1979a), a behavior which does not imply an ambushing predator. The web of *U. ochracea* is not exactly a sheet: the central thread is not wide and ribbon-like, but instead there are triangular

accumulations of fluid secretion at its emplacement, where most of the fluid secretion concentrates (PLACHTER, 1979a). Regarding predation, one can add that one species each of *Platyceridion, Proceroplatus* and *Truplaya* are ant-eating.

MAPPING THE ATTRIBUTES ON THE CLADOGRAMS

With the phylogenetic hypotheses for the groups involved, it is now possible to proceed to feeding habit optimization, first at the suprafamilial level, then for the Keroplatidae. At the suprafamilial level, we shall study three attributes, fungivory in its broad sense (as opposed to various other diets), endobiosis or epibiosis, and silk secretion. For the Keroplatidae, the four attributes studied are those indicated in Table 2, *e.g.* predation vs sporophagy (*Urytalpa* being considered a spore-feeder), highly acid pH vs less acid pH, net-web vs sheet-web, and optobiosis vs cryptobiosis.

Fungivory. The optimized cladogram (Fig. 11) suggests that the Ditomyiidae are truly primarily fungivorous (two lines have been drawn, since fungivory of several genera is not ascertained) and that fungivory *sensu lato* is most probably ancestral to the Sciaroidea + Cecidomyiidae lineage.

Epibiosis. All terminal taxa of the cladogram are endobionts except in the clade Keroplatidae-Diadocidiidae, where epibiosis may be assumed ancestral (Fig. 11). This way of life appeared independently in certain Mycetophilidae and Cecidomyiidae.

Silk secretion. For silk secretion, the optimized cladogram (Fig. 12) shows that its acquisition is ancestral for the Sciaroidea. A loss in the Ditomyiidae and one in Bolitophilidae, is more parsimonious (two steps) than an independent appearance in Keroplatidae-Diadocidiidae, in the Sciaridae+ clade and in the Cecidomyiidae (three steps).

Food preferences. The optimized cladogram on food preference (Fig. 13) shows that the ancestral condition of the Keroplatidae is predation, as hypothesized by ZAITSEV (1983) and MATILE (1986). Sporophagy has appeared twice, once in *Urytalpa* and once in the Keroplatini clade, but is not yet stabilized in *Cerotelion,* and perhaps *Mallochinus* (the only indication we have on the larval biology of this genus is that its habits correspond to that of *Keroplatus* as described by DUFOUR in 1839). Sporophagy is therefore a new specialization from predation. LASTOVKA'S hypothesis (1972), according to which predation probably evolved from sporophagy, is thus refuted.

Net-like web vs sheet-like web, and pH of web. Table 2 shows that these characters are correlated with the food preference of the larvae. Thus net-webs with a high acidity are ancestral

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FIGS 6-10. — Larvae of Keroplatidae in their webs. **6**: *Arachnocampa luminosa* (Skuse) (New Zealand) in a crevice of a cave wall with suspending lines, central tube and long fishing-lines. **7**: *Heteropterna chazeaui* Matile (New Caledonia) on the underside of a bracket-fungus; the larva hangs in a translucent sheet, only the central tube and attaching lines are visible. **8**: *Macrocera fasciata* Meigen (Europe) hanging from the ceiling of a quarry, with central thread and net-web with short fishing lines. **9**: *Cerotelion lineatum* (Fabricius) (Europe) on underside of a bracket-fungus; there are two central tubes, dense lines and no fishing lines. **10**: *Neoditomyia aerospicator* (Jackson) (Central America) under a leaf in tropical rain-forest, with suspending threads, central tube and fishing lines. Length of mature larvae: *A. luminosa,* 3-4 cm; *M. fasciata, N. aerospicator, C. lineatum,* 2,5-3 cm; *H. chazeaui,* 2-2,5 cm. Fig. from MATILE, 1990, except 10, a combination of a photograph of *N. aerospicator* by JACKSON (1974), and a sketch of attitude of larva of *N. andina* LANE in STÜRM (1973).
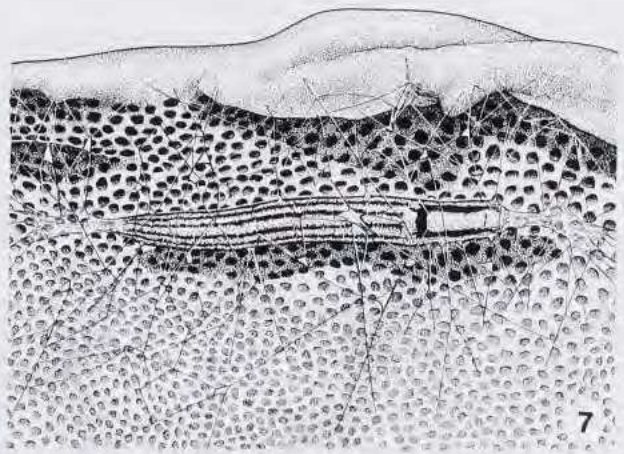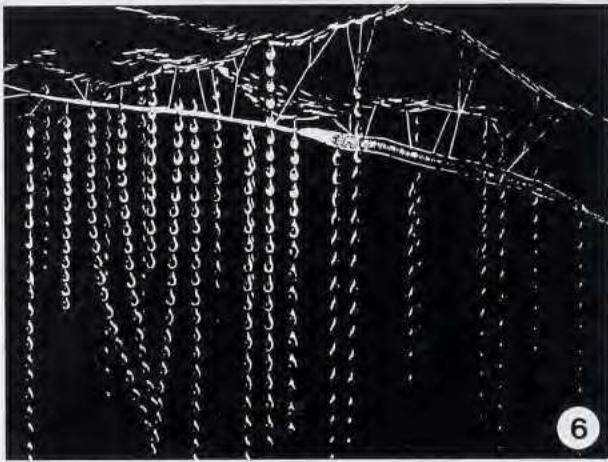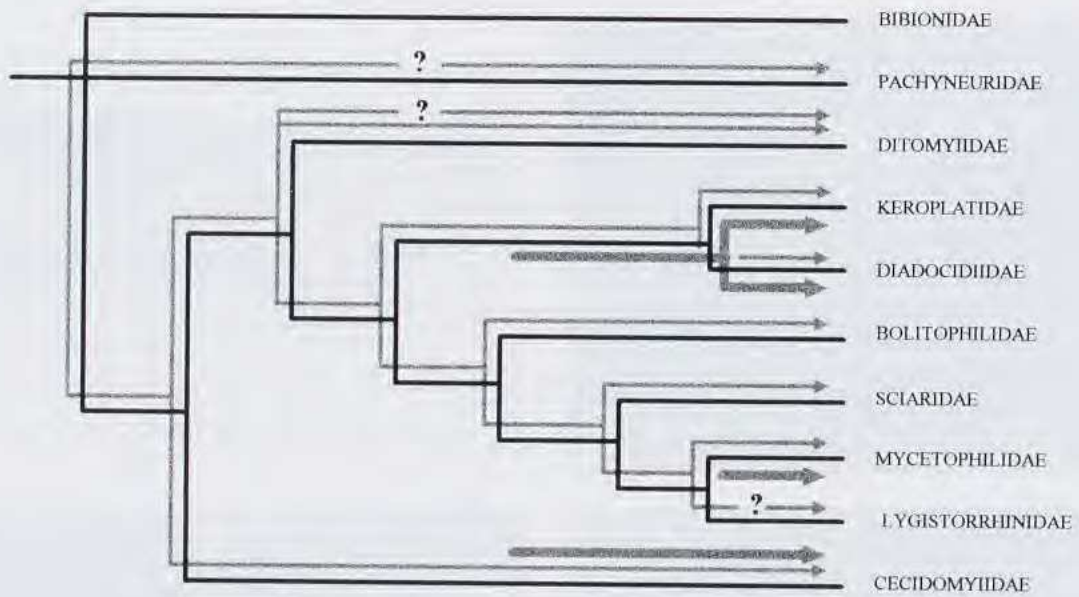
FIG. 11. — Evolution of fungivory *s.l.* (thin grey lines) and appearance of epibiosis (thick grey lines) in the Bibionomorpha.
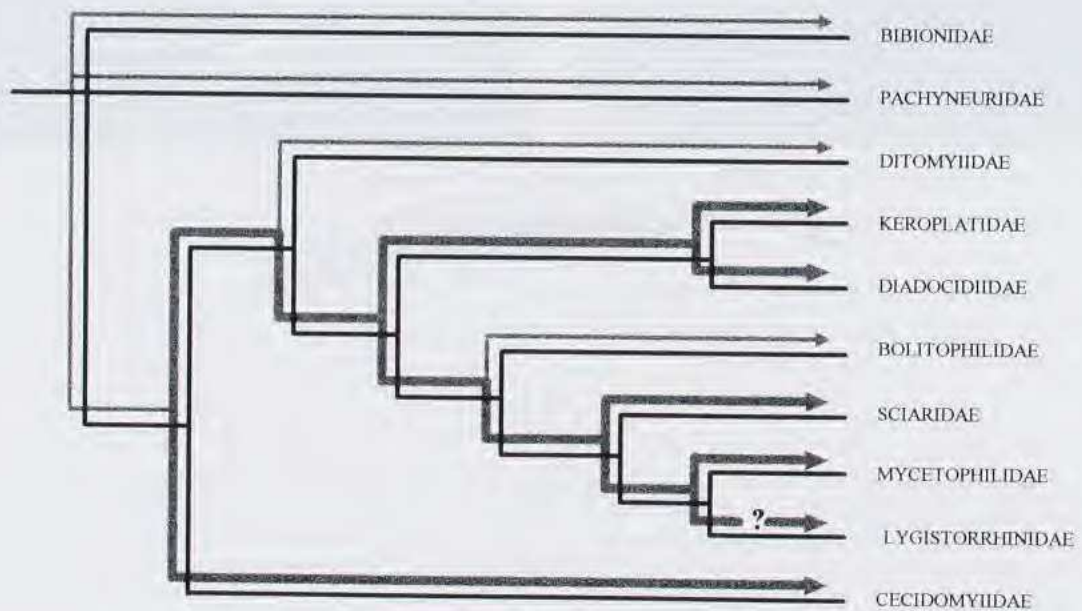
FIG. 12. — Absence (thin grey lines) or presence (thick grey lines) of silk secretion in the Bibionomorpha.
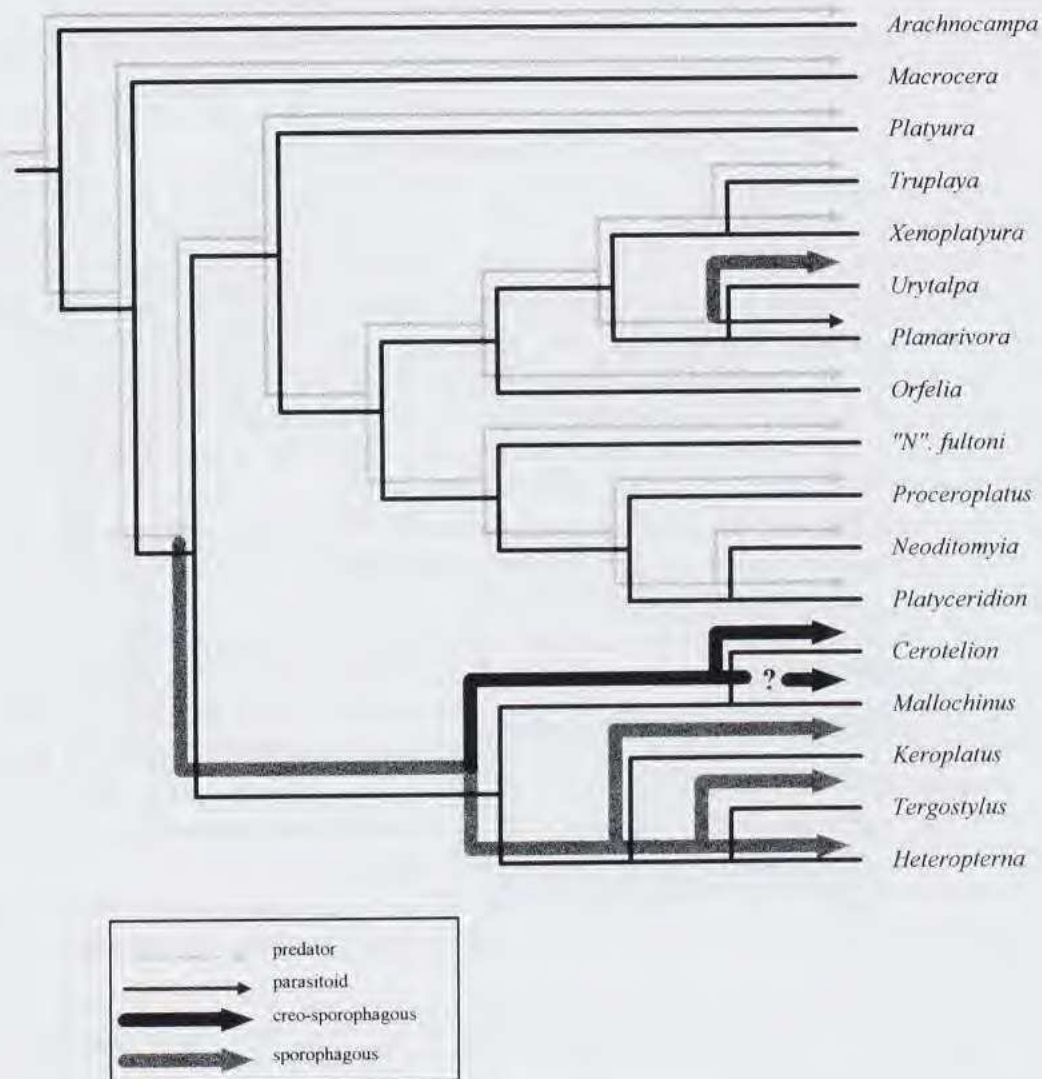
Fig. 13. — Food preferences of the known larvae of Keroplatidae.

for the Keroplatidae, while sheet-webs with low acidity are derived. These last features are characteristic of the Keroplatini clade and of the genus *Urytalpa*, and have appeared at least twice. PLACHTER's (1979c) hypothesis of plesiomorphy of the sheet-web is therefore refuted.

Cryptobiosis and optobiosis. As regards cryptobiosis and optobiosis, the superposition of these attributes on the cladogram (Fig. 14) gives two equally parsimonious scenarios (3 steps). If cryptobiosis is ancestral, tolerance to light must have appeared at least three times: in *Arachnocampa, Neoditomyia* and the Keroplatini. On the other hand, if optobiosis is ancestral, then cryptobiosis must have appeared independently once in *Macrocera* and once in the Orfeliini clade, with a reversal in *Neoditomyia*.

However, endobiosis is the ancestral condition of the Bibionomorpha, as shown on Fig. 11. Bibionid, pachyneurid and ditomyiid larvae live in closed, obscure and humid galleries, and we may therefore infer that cryptobiosis is the ancestral condition of keroplatids.

THE TEMPORAL DIMENSION

The study of the evolution of the attributes of the Bibionomorpha, and especially of the Keroplatidae, can be refined by taking into account the temporal dimension. The oldest Diptera are known from the Trias of Australia, North America and Europe (EVENHUIS, 1994; SHCHERBAKOV et al., 1996, and references in both works). As regards the recent families of Bibionomorpha, the earliest fossils are known from the Upper Triassic for the Bibionidae, the lower Jurassic for the Mycetophilidae, the Upper Jurassic for the Pachyneuridae, the Upper Jurassic/Lower Cretaceous for the Cecidomyiidae, the Lower Cretaceous for the Keroplatidae and the Sciaridae, the Eocene for the Ditomyiidae, and the Eocene/Oligocene for the Diadocidiidae and the Lygistorrhinidae (EVENHUIS, 1994).

The fossil data, mapped on the cladogram, and the principle of equal age of sister groups (Fig. 15), indicate that all the present families had appeared as such at least by the beginning of the Cretaceous, and more probably by the Upper Jurassic.

The optimization of silk secretion and predation on the cladogram is given in Fig. 16. Silk secretion must have appeared in the Sciaroidea clade at least by the Upper Jurassic. Its disappearance in Ditomyiidae must be at least pre-Eocene, from which the extant genus *Australosymmerus* Freeman is known. For Bolitophilidae, *Bolitophila* Meigen is known from Eocene-Oligocene, and the mesozoic fossils belong to the extinct genus *Mangas* Kovalev (perhaps not a Bolitophilidae at all), the larval biology of which is of course unknown; the loss of silk secretion cannot therefore be dated other than pre-Oligocene.

Regarding predation (Fig. 16), no data can be obtained from the optimized cladogram unless a further phylogenetic analysis is conducted for the three families in which it appeared independently.

Fungivory and epibiosis are mapped on figure 17. Fungivory, ancestral to the Sciaroidea, must have appeared at least by the Upper Jurassic. Epibiosis in the clade Diadocidiidae-Keroplatidae should be dated from the Lower Cretaceous, but its acquisition in Mycetophilidae and Cecidomyiidae cannot be dated without a further phylogenetic analysis of these families.

Fig. 18 combines the palaeontological and biogeographical data on the cladogram of the Keroplatidae. The two fossils appended to the *Macrocera* lineage represent two genera belonging to Macrocerinae, but of uncertain position inside the subfamily. These are *Schlueterimyia cenomanica* Matile, from the Upper Cretaceous, and an undescribed genus from the Lower Cretaceous (GRIMALDI, 1990). The biogeographical datings can be found in MATILE (1990), except for *Planarivora*. This genus has a southern transatlantic distribution – New-Zealand and South America – and thus can be dated at the latest from the Upper Cretaceous (MATILE, 1981b).

The optimized chronocladogram (Fig. 19) shows that the various food and web specializations of the family must have appeared at least by the end of the Lower Cretaceous, with the exception of the parasitoid habit, which dates from the Upper Cretaceous (assuming that the life-story of the neotropical species of *Planarivora* is the same as that of the Tasmanian
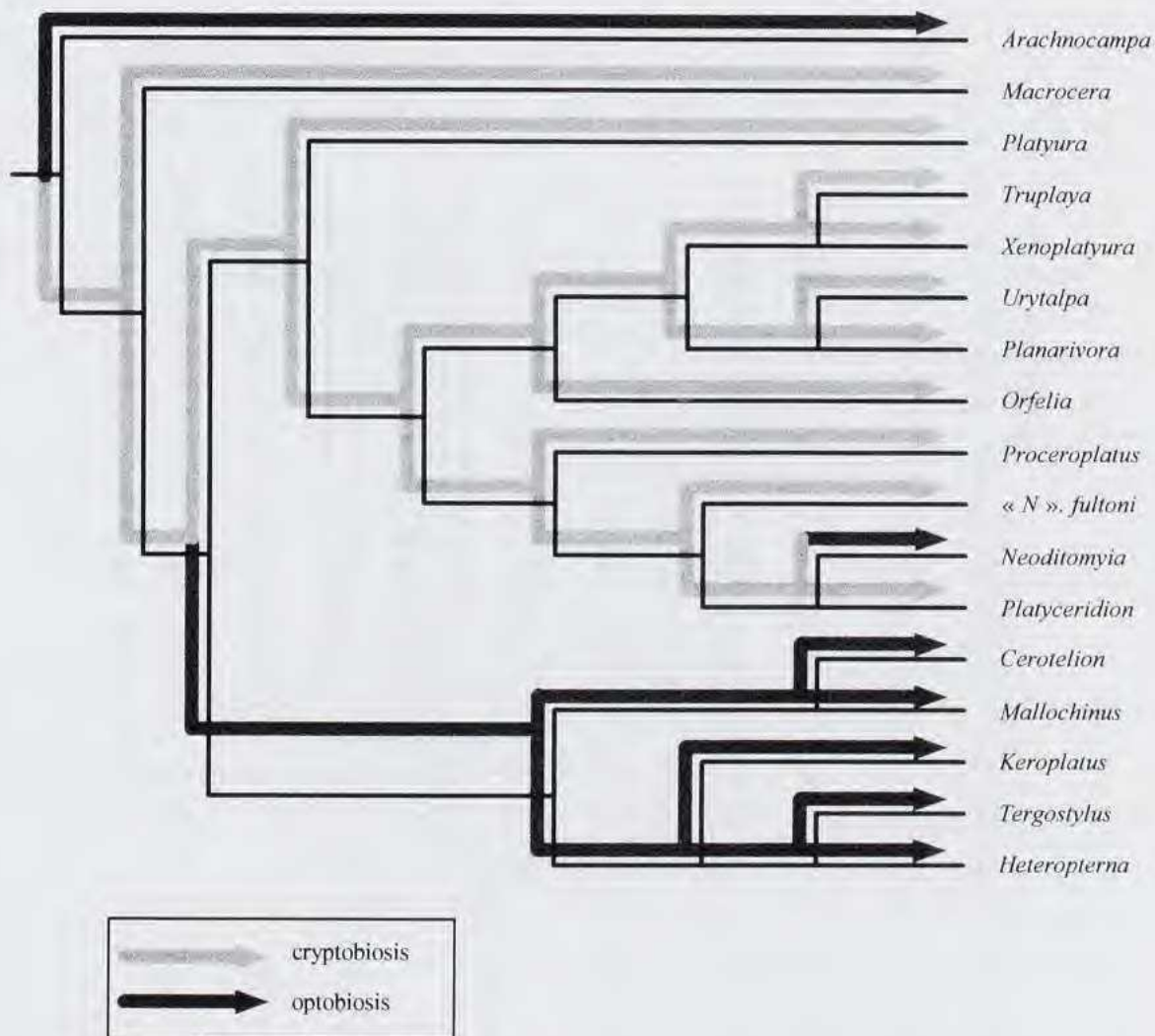
Fig. 14. — Distribution of cryptobiosis and optobiosis in the Keroplatidae.

species), and the independently acquired sporophagy of its sister-group *Urytalpa*, which may be presumed to be of the same age.

In the same way, the cladogram of the figure 20 demonstrates the origin of cryptobiosis in the Lower Cretaceous, and of optobiosis in Keroplatini at least at the end of the same period.

CONCLUSION

The optimization and dating of the cladograms allow inference of the ancestral larval state of the Bibionomorpha as an endobiont, as is the case for Sciaroidea, even if they contain numerous epibionts, which thus should have appeared more recently. Fungivory is another
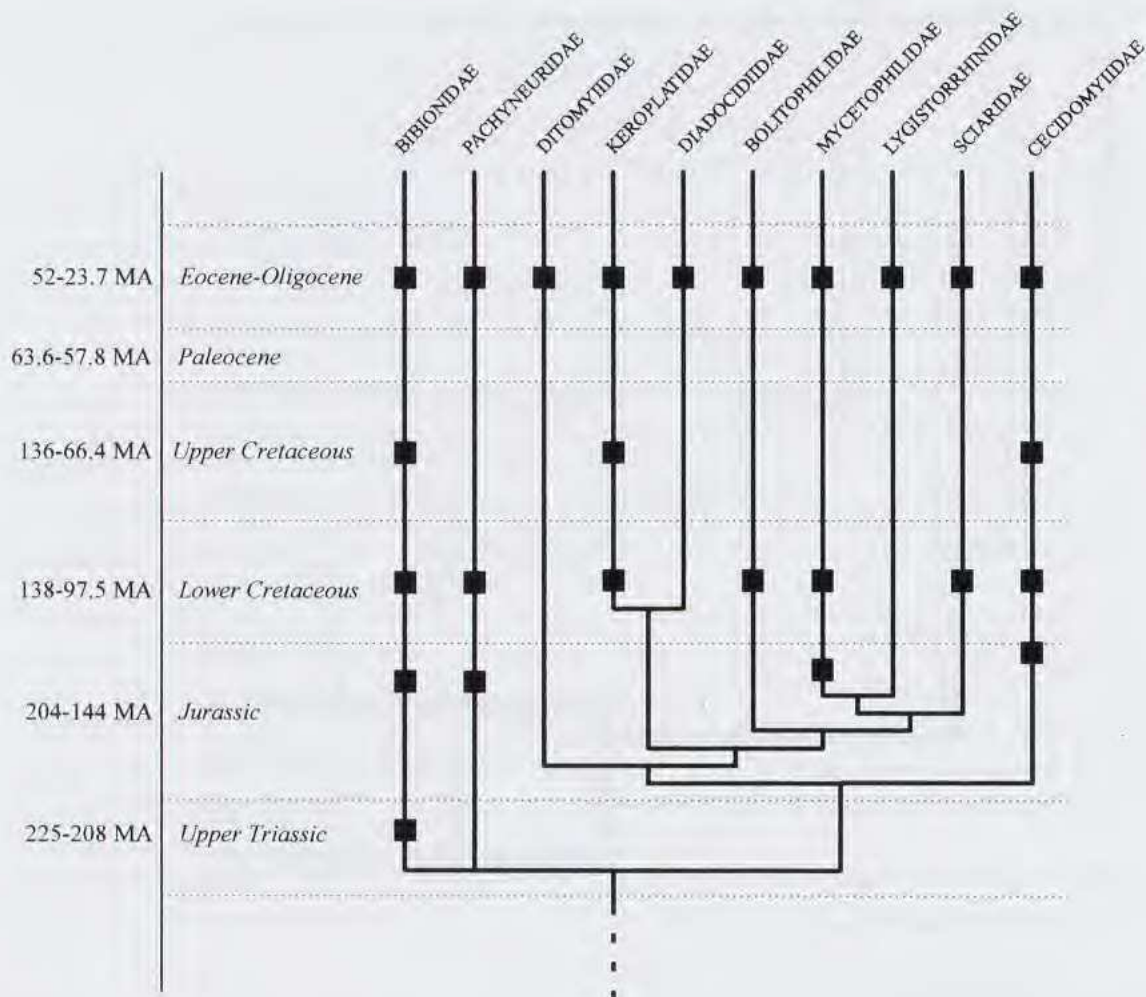
Fig. 15. — Pre-Miocene fossil data (black square) available on the taxa studied in this paper. BIB = Bibionidae; PAC = Pachyneuridae; DIT = Ditomyiidae; DIA = Diadocidiidae; KER = Keroplatidae; BOL = Bolitophilidae; MYC = Mycetophilidae; LYG = Lygistorrhinidae; SCI = Sciaridae; CEC = Cecidomyiidae. Geologic time scale after EVENHUIS (1994). For graphical reasons, no distinction has been made for Lower and Upper Jurassic.

ancestral trait of Sciaroidea, as supposed by most authors. ZAITSEV 's (1984) hypothesis of an epibiont ancestral larva for the fungicolous clades is thus refuted. The endobiosis and fungivory of the ancestral Sciaroidea is corroborated by their larval morphology. The larvae of this superfamily are indeed deprived of the anatomical tools necessary for predation: their antennae are most often reduced to a cupule with a few sensillae, their organs of vision are rudimentary, and they have no well-developed sensorial macrochaetae. This kind of morphology is not that of a predator, but of an animal living in the middle of an important amount of food, as noted by
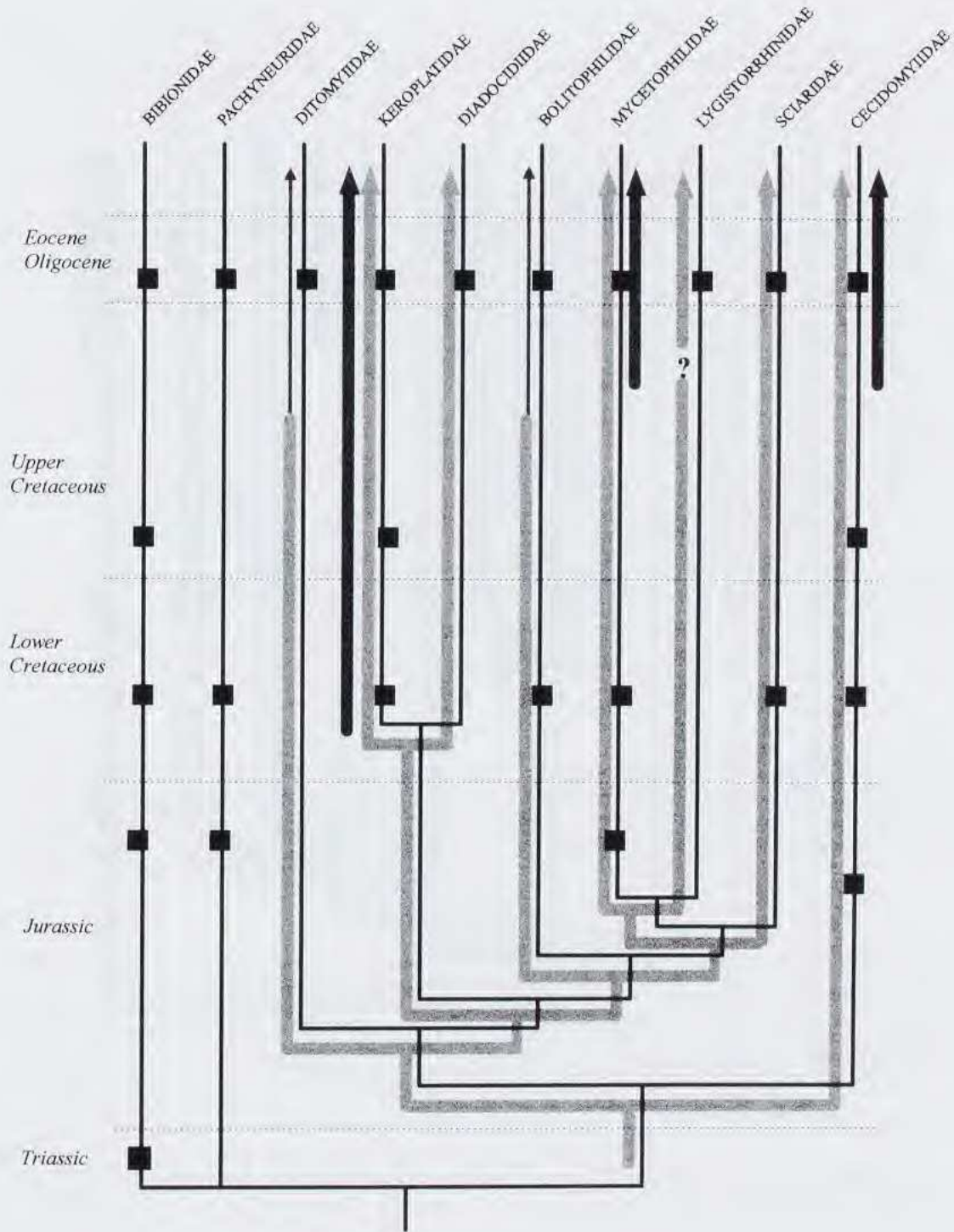
Fig. 16. — Temporal evolution of silk secretion (thick light grey lines) and predation (thick dark grey lines) in the Bibionomorpha. Black squares: pre-Miocene fossil data.
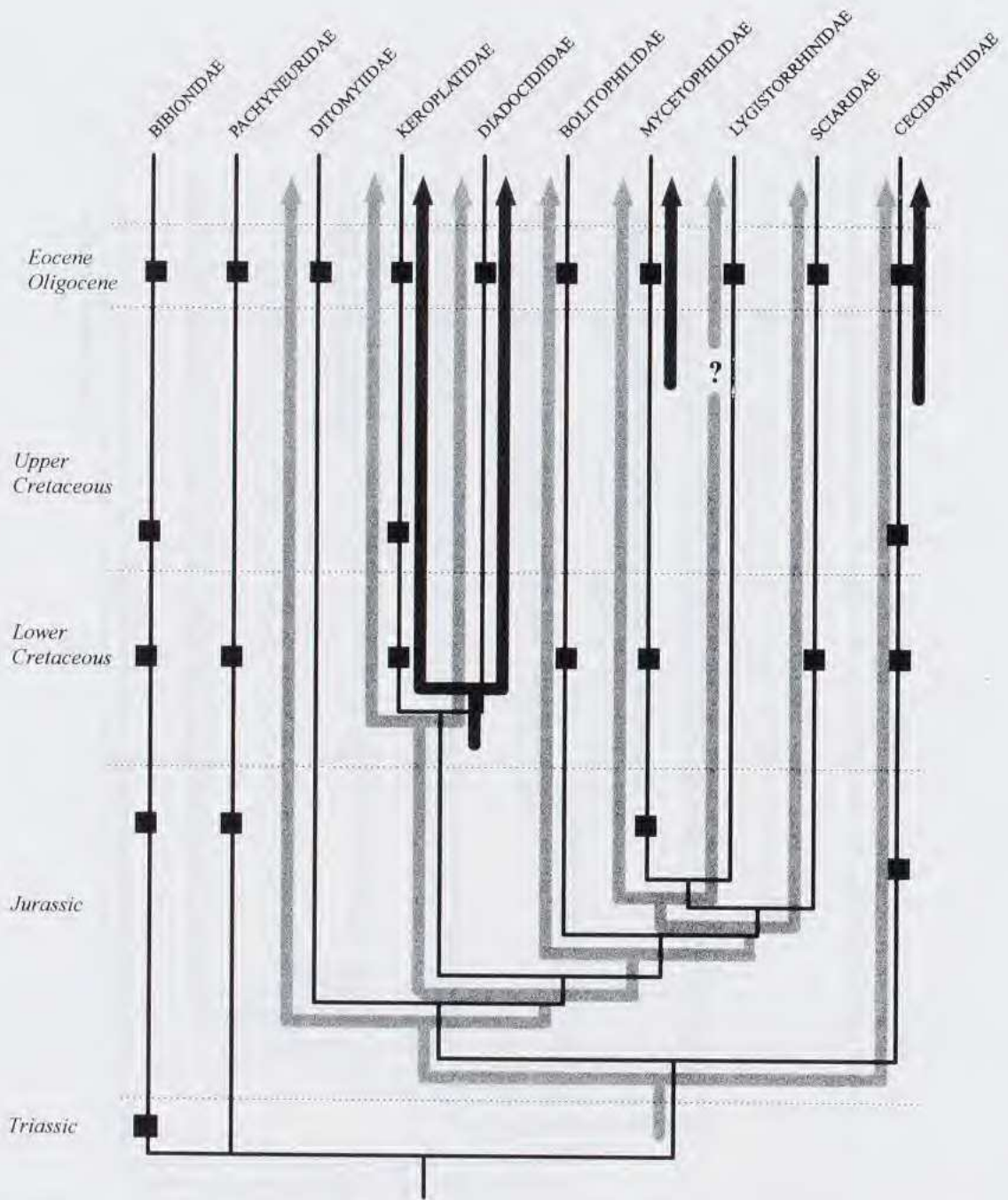
Fig. 17. — Temporal evolution of fungivory (light grey lines) and epibiosis (dark grey lines) in the Bibionomorpha. Black squares: pre-Miocene fossil data.

MAMAEV (1968, 1975) for the Cecidomyiidae. The Keroplatidae and Diadocidiidae are epibionts but nevertheless possess this endobiont morphology.
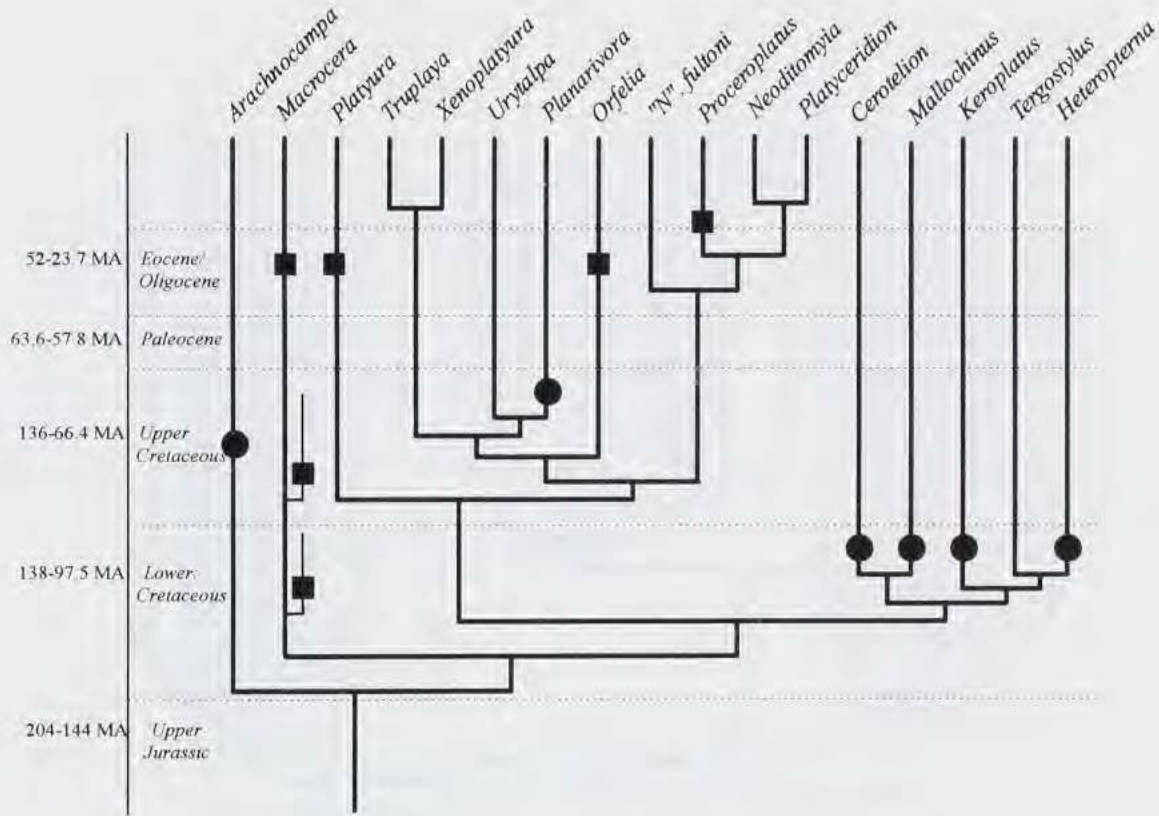
Fig. 18. — Pre-Miocene fossil data (black square) and biogeographical data (black disk) available on the taxa studied in this paper. *Ara = Arachnocampa; Mac = Macrocera; Pla = Platyura; Tru = Truplaya; Xen = Xenoplatyura; Ury = Urytalpa; Plan = Planarivora; Orf = Orfelia; Neo = Neoplatyura; Pro = Proceroplatus; Neod = Neoditomyia; Plat = Platyceridion; Cer = Cerotelion; Mal = Mallochinus; Ker = Keroplatus; Ter = Tergostylus; Het = Heteropterna.* Geologic time scale after EVENHUIS (1994).

Silk secretion is apomorphic for Sciaroidea; it appeared during the Jurassic and was subsequently lost in Ditomyiidae and Bolitophilidae. Epibiosis occurred at least three times, once in the clade Keroplatidae-Diadocidiidae, once in Mycetophilidae and once in Cecidomyiidae.

Cryptobiosis is apomorphic for the Keroplatidae, and appeared in the Lower Cretaceous, while optobiosis arose independently three times, once in the Keroplatini during the Lower Cretaceous, once in *Arachnocampa* at least by the Upper Cretaceous, and once again in *Neoditomyia*, probably at a much later time, during the Miocene.

Predation arose once in the Keroplatidae at some time during the Lower Cretaceous, and at least twice, at an undetermined period, in Mycetophilidae and Cecidomyiidae. The net-like web of the predator forms is not derived from the sheet-like web, as assumed by PLATCHER (1979c), but the opposite.
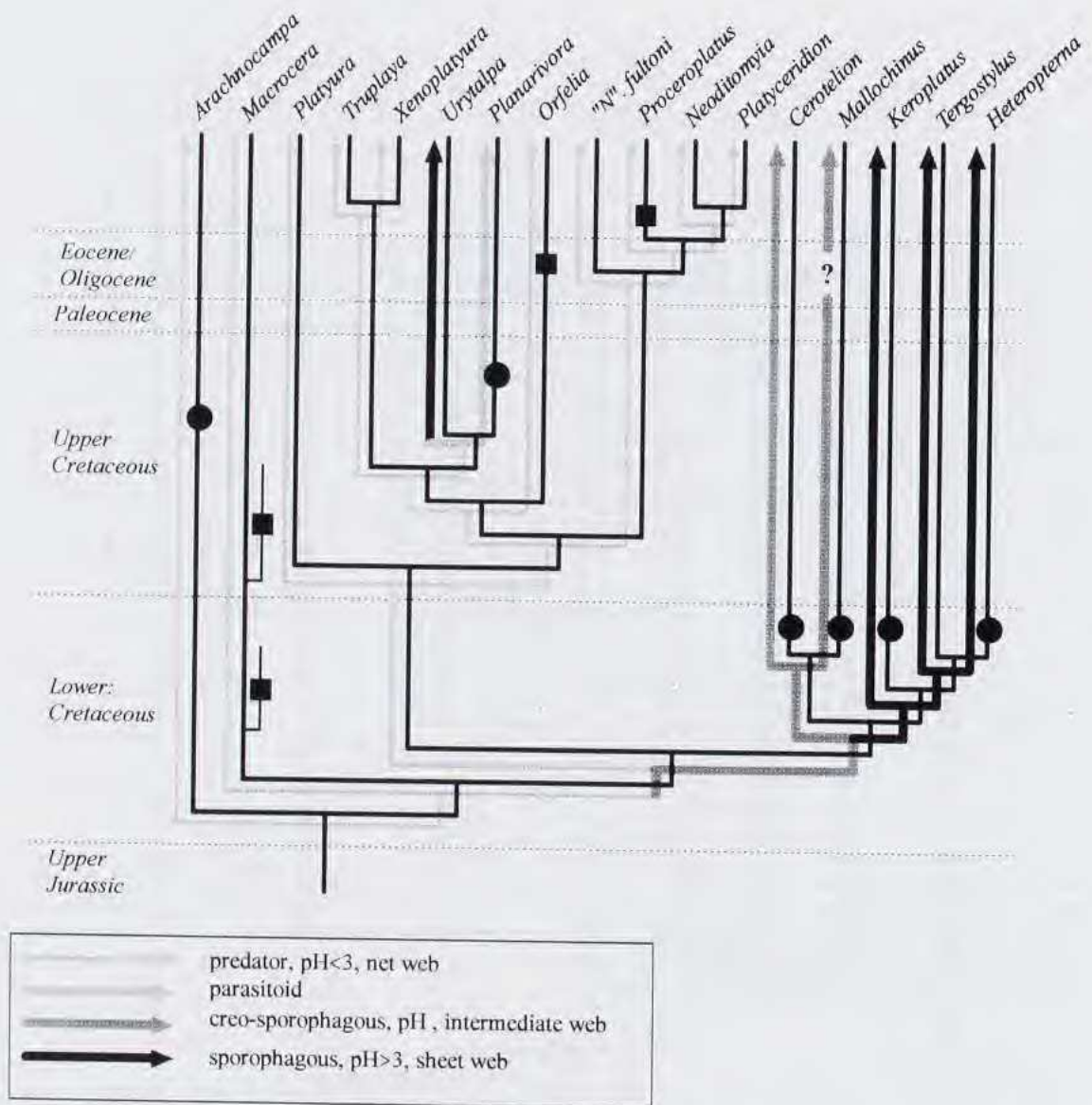
Fig. 19. — Temporal evolution of food preference in the Keroplatidae. See fig. 18 for abbreviations.

Sporophagy in Keroplatidae arose twice, once in the Lower Cretaceous (clade Keroplatini), and once probably in the Upper Cretaceous (genus *Urytalpa*). In these groups, sporophagy seems correlated with a sheet-like web and a labial fluid with a pH of 3 or more. The sporophagy of these Keroplatidae is derived from a predatory diet, and not the opposite as assumed by LASTOVKA (1972). It is not therefore homologous to the "ordinary" fungivory found in other Sciaroidea.
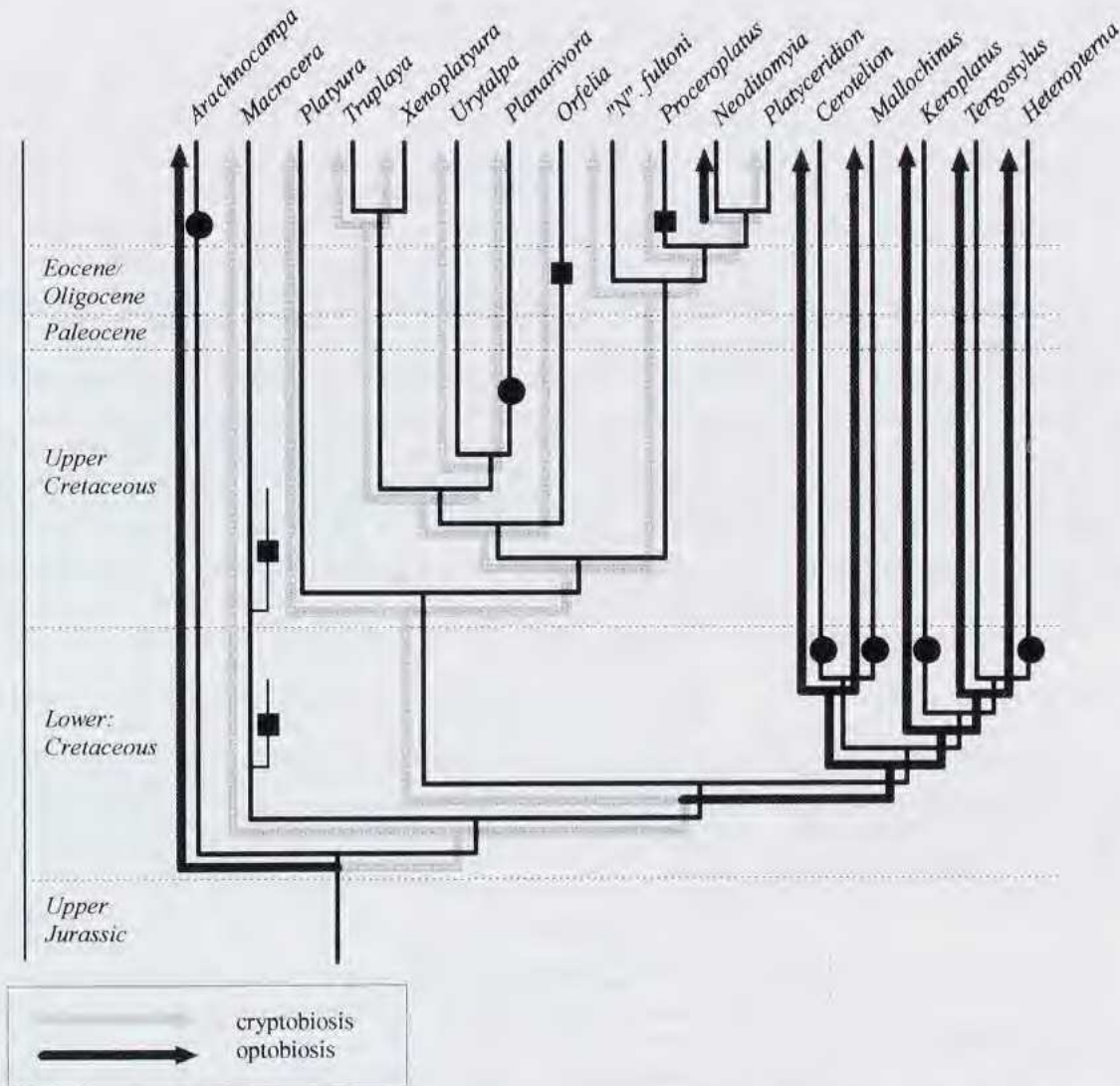
Fig. 20. — Temporal evolution of cryptobiosis and optobiosis in the Keroplatidae. See fig. 18 for abbreviations.

We may consider the ancestral larval stock of the Sciaroidea as an endobiont fungicolous insect, without silk secretion, perhaps living as far back as the Upper Jurassic - fossil Sciaroidea have been described as early as the Lower Jurassic (see KALUGINA & KOVALEV, 1985; KOVALEV, 1987b), and of these at least the Pleciofungivoridae certainly are correctly placed in the superfamily. The keroplatidian clade, the larvae of which have an endobiont morphology (antennae, eyes and other sensorial organs reduced, scraper mouthparts), became epibionts during the Lower Cretaceous and were then able to exploit at the best their silk- and oxalic-secreting capacity and adopt a predatory diet - making up for the lack of predatory organs by an extension of the body: the hunting net-web. The extension of the net-web to a sheet-web, an

intermediary state of which still can observed in *Cerotelion*, and a variant in *Urytalpa*, allowed them to switch to a new food source: the collecting of bracket fungi spores.

The most important problem posed by the hypothesis of Cretaceous sporophagy in Keroplatini is that the oldest and certain fossil Polyporaceae are only known from the Miocene. Some "bracket-fungi" have been described from earlier periods, back to the Carboniferous, but that they really belong to Polyporaceae is apparently still disputed. Nonetheless, the genus *Fomites*, described from the Lower Miocene of Lybia, is closely allied with the present genus *Fomes* (LOCQUIN & KOENIGER, 1981), and the ancestral stock of the Polyporaceae should therefore be much older. If the present hypothesis is founded, this family of fungi should have appeared at least by the Lower Cretaceous.

Although we know many fossils of Bibionomorpha from the Lower and Middle Jurassic, none is close to the Keroplatidae. One may therefore think that the acquisition of all these attributes occurred during a very short period of time, no more than a few tens of MY, between the end of the Jurassic and the beginning of the Lower Cretaceous. It was followed by a stasis more than 100 MY long, marked only by the divergence of the clade *Urytalpa-Planarivora* towards sporophagy for the first, parasitism for the second, probably during the Upper Cretaceous.

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APPENDIX 1. — List of the characters used in the study of the Sciaroidea (plesiomorphic state: 0; apomorphic states: 1, 2) (WB = WOOD & BORKENT, 1989; LM = MATILE, 1990; OC = OOSTERBROECK & COURTNEY, 1995) and character matrix.

Larva (unknown for Lygistorrhinidae)
1. Antennae: with several segments: 0. Antennae one-segmented, cylindrical or disc-like: 1 (LM: 386, char. 9, for Bolitophilidae; OC: 295, char. 15).
2. Frontoclypeal apotome: short, not extended to posterior margin: 0. Frontoclypeal apotome long, extending to posterior margin of head capsule: 1 (LM: 385, char. 2).
3. Posterior tentorium as a rod independent from the head capsule from the metatentorina on: 0. Posterior tentorium laterally fused with the head capsule, forming a transverse bridge, unsclerotinized at least at middle: 1. The "posterior bridge" of the Sciaroidea is here interpreted as homologous to the posterior tentorium, as demonstrated by its muscles insertion and the discovery of the metatentorina (MATILE, 1967, 1990; see also discussion in OC: 308, char. 101). The condition is variable in Cecidomyiidae (*cf.* MAMAEV & KRIVOSHEINA, 1965, 1993).
4. Anterior tentorial arms: strong: 0. Anterior arms thread-like: 1 (see discussion in OC: 308, char. 02). The condition is variable in Cecidomyiidae.
5. Maxillae: pyramidal: 0. Maxillae flattened and strongly sclerotinized: 1. TESKEY (1981) has pointed out that the maxillae of Nematocera are mostly membranous and passive, and that "a notable exception" was found in the larvae of Sciaroidea. In fact, maxillae of Ditomyiidae resemble closely those of Bibionidae (see also discussion in WB: 1353).
6. Maxillae: cardo free: 0. Cardo fused or closely apressed to anterior margin of head capsule: 1 (WB: 1351, char. 27; OC: 296, char. 25).
7. Maxillary palpus jutting out: 0. Palpus reduced, flush with the maxilla: 1 (WB: 1356, char. 45, in analysis of Psychodomorpha; LM: 385, char. 3; OC: 296, char. 26).
8. Mandible of the ordinary, pyramidal sort: 0. Mandible as a half-circle, toothed at margin, one or more rows of spinules: 1. Character not formally included in LM analysis, but dicussed p. 386.
9. Body cylindrical, more or less flattened: 0. Body strongly constricted: 1. In Bibionomorpha, the state 1 of this character exists only in Pachyneuridae and Ditomyiidae, and I think it is an adaptation to life in wood or ligneous bracket-fungi, therefore apomorphic.
10. Subanal region without appendices or macrochaetae: 0. Subanal region with one or the other: 1. Same than character 9.
11. Metathoracic spiracle present: 0. Metathoracic spiracle absent: 1 (WB: 1351, char. 30).
12. Abdominal spiracle VIII present: 0. Spiracle VIII absent: 1 (STEFFAN, 1981; LM: 385, char. 4).
13. Other abdominal spiracles: present and open: 0. Abdominal spiracle absent or closed (1). (LM: 385, char. 6).
14. Tracheal system: at least 5 dorsal transverse connectives: 0. At most one connective: 1 (OC: 302, char. 53). State of character unknown in Pachyneuridae and Bibionidae.

Pupa (unknown for Lygistorrhinidae)
15. Prothoracic horns large: 0. Prothoracic horns small: 1. Character not formally included in LM analysis, but discussed p. 385. Thoracic horns are well developed in Bibionidae, Ditomyiidae and Cecidomyiidae, as well as in most other Nematocera (see f. ex. BRAUNS, 1954b).

Imago
16. Ocular bridge: absent: 0. Ocular bridge present: 1 (WB: 1352, char. 33). The condition is variable in Ditomyiidae and Mycetophilidae, where a few genera have an ocular bridge; see also discussion in OC: 309, char. 104. Some Sciaridae and Cecidomyiidae have no eye-bridge, but this is obviously a loss, and the character has been coded 1 in these two families.

17. No tibial spurs II-III: 0. Tibial spurs present: 1. Spurs II-III are absent in some genera of Mycetophilidae, Keroplatidae and Sciaridae; this is again obviously a loss, and the charcater has been coded 1 in these three families. See discussion in LM: 418, A.3.3.
18. Vein R4 long: 0. R4 short or absent: 1 (LM: 385, char. 1; also: 434, A.4.5.8.).
19. Two basal cells: 0. One basal cell: 1. This polarisation is obvious from the dipterous wing groundplan; see for example McALPINE, 1981: 31 & *ff.*
20. Transverse *tb* subvertical: 0. *tb* longitudinal: 1 (LM: 386, char. 5; also: 426, A.4.5.).
21. Transverse *ta* subvertical: 0. *ta* longitudinal: 1 (LM: 386, char. 8; also.: 426, A.4.5.). The condition of this transverse, when recognizable, is variable in Cecidomyiidae.
22. Transverse *mcu* present: 0. *mcu* absent: 1 (LM: 386, char. 7).
23. Costa continuous around wing: 0. Costa abbreviated at apex of wing: 1 (OC: 304).
24. Insertion of abdomen on thorax wide: 0. Insertion narrow: 1. Insertion very narrow: 2 (LM: 386, char. 12; also p. 379-383).
25. Mediotergite partly included in abdominal segment I: 0. Mediotergite free: 1. Character not formally included in LM analysis, but dicussed p. 379-383.
26. Laterotergite narrow: 0. Laterotergite wide: 1 (LM: 386, char. 11).
27. Coxae short: 0. Coxae long: 1. See discusssion in LM: 413, A.3.1.
28. Sclerotized part of aedeagus tubular: 0. Aedeagus flattened: 1 (WOOD, 1991; OC: 307, char. 92).
29. Somatic and germ cells with same number of chromosoms: 0. Some chromosomes eliminated in somatic cells: 1 (WB: 1352, char. 32; OC: 307, char. 98). State of character known only in some species of Sciaridae and Cecidomyiidae, and one species of Mycetophilidae.
30. Central microtubule of sperm tail present: 0. Central microtubule absent: 1. (OC: 307 , char. 95 – polarity inversed in text, but not in character matrix). Keroplatidae polymorphic (coded ?). State of character unknown in Bibionidae, Pachyneuridae, Ditomyiidae and Lygistorrhinidae.

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                   12345678911111111122222222223
                   01234567890123456789 0
Bibionidae         0000000000000?00100000000000??
Pachyneuridae      0000000011100?00100000000000??
Ditomyiidae        0011011011100001010001110111??
Diadocidiidae      11111110001110101110001111111??
Keroplatidae       1111111000111010110001211111??
Bolitophilidae     1111111100110010111100111101??
Mycetophilidae     11111111001100171111111121111100
Lygistorrhinidae   ???????????????011111112111??
Sciaridae          1111111000110111111111110010111
Cecidomyiidae      00??01000010010101117100000111
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APPENDIX 2. — List of the characters used in the study of the subfamilies of Keroplatidae and tribes of Keroplatinae (plesiomorphic state: 0; apomorphic state: 1; LM = MATILE, 1990) and character matrix.

Larva
1. Head capsule short and round: 0. Head capsule short and rectangular: 1. Head capsule long and narrowed in middle: 2 (LM: 473).
2. Anterior tentorial arms very thick: 0. Anterior tentorial arms reduced: 1. Anterior tentorial arm strongly reduced: 2.
3. One pair of stemmata: 0. Two pairs of stemmata: 1 (LM: 474).
4. Antennae small: 0. Antennae large, reaching almost middle of genae: 1 (LM: 475).
5. No lateral labral lobes: 0. Two labral lateral lobes: 1 (LM: 475).

6. Maxillary cardo normal: 0. Maxillary cardo strongly lenghtened: 1 (LM: 475).
7. Mandibles short, Bibionid-like: 0. Mandibles long and narrow: 1 (LM: 371).
8. Larva hemipneustic: 0. Spiracles absent or non fonctional: 1 (LM: 371).
9. Abdominal spiracles present, either opened or closed: 0. No abdominal spiracles: 1 (LM: 477).
10. Malpighian tubules normal 0. Malpigian system cryptonephridian: 1 (LM: 371).
11. Oesophagus short: 0. Oesophagus as long as middle gut: 1 (LM: 371).
12. SII sensilla present: 0. SII sensilla absent: 1 (LM: 371).
13. Abdomen smooth, without hypodermal colored bands: 0. Abdomen finely annelated, with colored hypodermal bands: 1
    (LM: 371).
14. No luminous organ, or a simple luminous organ linked to fat body or black bodies: 0. A complex luminous organ formed
    by the Malpighian tubules and a tracheal reflector: 1 (LM: 477).

Pupa
15. Nototheca simple: 0. Nototheca with a sagittal crest: 1 (LM: 473).

Imago
16. Foramen magnum in dorsal position: 0. Foramen magnum in central position: 1 (LM, 1990: 387).
17. Mediocellar sclerite absent: 0. mediocellar sclerite présent: 1 (LM: 389).
18. No cerebral sclerite: 0. A cerebral sclerite: 1 (LM: 388).
19. Antennae simple: 0. Antennae thickened or pectinated: 1 (LM: 395). The state of character is variable in Orfeliini.
20. Postmentum present: 0. Postmentum absent: 1 (LM: 398). The condition is variable in Orfeliini.
21. Four palpomeres, if less than 4 the last one not thickened and porrect: 0. One or two palpomeres, the last one thickened
    and porrect: 1 (LM: 397).
22. Presternite present: 0. Presternite absent: 1 (LM: 401).
23. Transverse suture complete: 0. Transverse suture incomplete: 1 (LM: 402).
24. Postpronotum lateral and distinct: 0. Postpronotum dorsal, more or less fused with praescutum: 1 (LM: 399).
25. Mesepimeron almost as wide ventrally than dorsally: 0. Mesepimeron narrow or absent ventrally: 1 (LM: 411).
26. Metepimeron almost as wide as high: 0. Metepimeron much wider than high: 1 (LM, 1990: 412; the epimeron and
    episternite have been inadvertently inversed while lettering fig. 1080-1087).
27. Laterotergite narrow and subvertical: 0. Laterotergite wide and and oblique: 1 (LM, 1990: 406).
28. Alular incision present: 0. Alular incision absent: 1 (LM, 1990: 426; the presence of an alular incison is here considered as
    the groundplan of Sciaroidea, its disappearance in *Arachnocampa* and *Bolitophila* a reversal).
29. Costal vein extending after apex of wing: 0. Costa shorter: 1 (LM, 1990: 431).
30. R4 present or absent, R1 and R5 close to one another: 0. R4 absent, and at the same time R1-R5 widely separated: (LM:
    435).
31. No radiomedian coaptation: 0. A radiomedian coaptation: 1 (LM: 436). State variable in Ditomyiidae.
32. Basal and *ta* transverse fused: 0. Basal transverse distinct from *ta*: 1 (LM: 438).
33. Coxae of about the same length: 0. Coxae I longer than the two other pairs: 1 (LM: 414).
34. Tibiae bearing macrochaetae: 0. No tibial setae: 1 (LM: 417).
35. Tibiae II-III with apical combs: 0. No apical tibial combs: 1 (LM: 421).
36. A pair of spiracle on abdominal segment I: 0. No abdominal spiracles I (LM: 448).
37. male: segment VIII about half as long as VII: 0. Segment VIII shorter, more or less retracted under VII: 1 (LM: 450).
38. male: Hypoproct complete or membranous, but not notched basally: 0. Hypoproct deeply notched basally: 1 (LM: 452).
39. male: Sternite IX distinct: 0. Sternite IX fused or lost: 1 (LM: 456).
40. male: Tergite X present: 0. Tergite X absent: 1 (LM: 451). Condition ambigous in Ditomyiidae (LM: 452).
41. male: Ejaculatory apodeme developed: 0. Ejaculatory apodeme reduced to a dorsal rod: 1 (LM: 469).
42. female: Tergite VIII entire or weakly reduced: 0. Tergite VIII strongly reduced or membranous, invaginated under VII: 1
    (LM: 471)
43. female: Sternite VIII complete basally: 0. Sternite VIII completely separated in two halves: 1 (LM: 471).
44. female: Tergite IX entire: 0. Tergite IX reduced: 1. Tergite IX entirely membranous: 2 (LM: 471).
45. female: Cerci two-segmented: 0. Cerci one-segmented: 1 (LM: 472).

	12345678911111111122222222222333333333344444401234567890123456789012345678901234567890123456789012345
Ditomyiidae	0000000000000000000000011110000?00001100?00000
Arachnocampinae	201000111111111110010100000101010000001011000
Marocerinae	110111110111100001000011010101011011010010
Keroplatini	110010110111100000101011110101000011110100111
Orfeliini	110010110111100000??001111101010001110100101

APPENDIX 3. — List of the characters of 5 genera of Keroplatini (plesiomorphic state: 0; apomorphic states: 1, 2; LM = MATILE, 1990) and character matrix

Imago

1. Eyes not or slightly emarginated above antennae: 0. Eyes strongly emarginated: 1 (LM: 390).
2. Antennal scape beakless: 0. Antennal scape with a beak: 1 (LM: 394).
3. Four palpomeres: 0. Two palpomeres: 1. One palpomere: 2. (LM: 396).
4. Mouthparts long, jutting out from the lower eye margin: 0. Mouthparts short, not jutting out from eye margin: 1 (LM: 398).
5. Scutellum haired on entire disk: 0. A pair of discal setae: 1. Scutellum bare on disk: 2 (LM:　404).
6. Laterotergite haired: 0. Laterotergite bare: 1 (LM: 407).
7. Tibial setuale irregular: 0. Tibial setae in regular rows: 1 (LM: 416).
8. Abdomen with an intercalar sclerite: 0. No intercalar abdominal sclerite: 1 (LM: 450).
9. male: abdomen cylindrical: 0. Abdomen flattened: 1 (LM: 445).
10. male: tergite IX as a flat plate: 0. Tergite IX expanded laterally: 1 (LM: 445).
11. male: hypoproct at least partially sclerotinized: 0. Hypoproct entirely membranous: 1 (LM: 452).
12. male: perigonostylar bridge complete: 0. Perigonostylar bridge incomplete: 1 (LM: 458).
13. male: inner margin of gonostyle not more sclerotinized than rest of appendice: 0. Inner margin of gonostyle strongly sclerotinized and denticulated: 1 (LM: 466).
14. female: sternite VIII infolded at most on basal half: 0. Sternite VIII infolded at least at ¾ of its length: 1 (LM: 471).

	1234567891111101234
Arachnocampa	00002000000000
Cerotelion	11101100000010
Mallochinus	11101000000010
Keroplatus	01100011101101
Tergostylus	00210111111101
Heteropterna	00210111110101

APPENDIX 4. — List of the characters used in the study of 10 genera of Orfeliini (plesiomorphic state: 0; apomorphic states: 1, 2; (LM= MATILE, 1990) and character matrix

Imago

1. Antennae threadlike: 0. Antennae pectinated ou serrulated: 1 (LM: 395).
2. 4 palpomeres: 0. Three palpomeres or less: (LM: 396).
3. Three ocelli: 0. Two ocelli: (LM: 389).
4. No parachrostical stripes: 0. Two wide parachrostical stripes: 1 (LM: 403).
5. Prospiracular setae present: 0. Prospiracular setae absent: 1 (LM: 410).
6. Mediotergite rounded at apex: 0. Mediotergite strongly angulous: 1 (LM: 405).
7. Laterotergite setiferous: 0. Laterotergite bare: 1 (LM: 407).

8. Mesanepisternite setiferous: 0. Mesanepisternite bare (LM: 410).
9. Metanepisternite setiferous: 0. Metanepisernite bare: 1 (LM: 412).
10. C continuing widely after tip of R5: 0. C stopping at tip of R5, or a little farther: 1 (LM: 431).
11. M2 and M3 entire: 0. M2 et M3 interrupted before wing margin: 1 (LM: 438).
12. Basis of M present as a true vein: 0. Basis of M absent or present as a fold: 1 (LM: 438).
13. Radiomedian fusion bearing setulae: 0. Radiomedian fusion bare: 1 (LM: 438).
14. Lower veins haired dorsally: 0. Lower veins bare:1 (LM: 442).
15. Anal vein long: 0. Anal vein short: 1 (LM: 441).
16. Tibial setulae irregular: 0. In regular rows: 1. Some darker rows of closely set setulae: 2 (LM: 416).
17. Outer tibial spurs II-III long: 0. Outer tibial spurs II-III reduced: (LM: 418).
18. male: abdomen cylindrical: 0. Abdomen petiolated and laterally compressed: 1 (LM: 445).
19. male: hypopygium capable of rotation: 0. hypopygium non rotatable: 1 (LM: 67, 451).
20. male: Tergite IX long or short, but as a dorsal plate: 0. Tergite IX long or very long, strongly expanded laterally: 1 (LM: 456)
21. male: aedeagus short: 0. Aedeagus long, extending at least to tergite VII (LM: 469).
22. male: gonostyles with one segment, either divided or not: 0. Gonostyles at least two-segmented: 1 (LM: 465).
23. male: gonocoxites approximated ventrally: 0. Gonocoxites widely separated ventrally, the aperture closed by a ventral desclerotized process: 1 (LM: 461).

	1234567891111111112222
	01234567890123
Arachnocampa	00011001110001000000000
Platyura	00011011110010000000000
Orfelia	00001111100101120000010
Neoditomyia	10100000100101111000000
Xenoplatyura	00001111001101000111111
Urytalpa	00011011110100000111100
Truplaya	00000111111010101111111
Proceroplatus	10001000100111011000000
Platyceridion	1110100010?111011000010
Planarivora	01010110100110000011110
"N." fultoni	10001010100111010010000